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## SCIENCE

# Distribution of fossil marine vertebrates in Cerro Colorado, the type locality of the giant raptorial sperm whale *Livyatan melvillei* (Miocene, Pisco Formation, Peru)

Giovanni Bianucci[a*], Claudio Di Celma[b], Walter Landini[a], Klaas Post[c], Chiara Tinelli[a], Christian de Muizon[d], Karen Gariboldi[a,e], Elisa Malinverno[f], Gino Cantalamessa[b], Anna Gioncada[a], Alberto Collareta[a,e], Rodolfo-Salas Gismondi[g], Rafael Varas-Malca[g], Mario Urbina[g] and Olivier Lambert[h]

[a]*Dipartimento di Scienze della Terra, Università di Pisa, Via Santa Maria, 53, Pisa 56126, Italy;* [b]*Scuola di Scienze e Tecnologie, Università di Camerino, Camerino 62032, Italy;* [c]*Natuurhistorisch Museum Rotterdam, P.O Box 23452, Rotterdam 30001, The Netherlands;* [d]*Département Histoire de la Terre, (CR2P – CNRS, MNHN, UPMC, Sorbonne Université) Muséum national d'Histoire naturelle, 57 rue Cuvier, Paris 75005, France;* [e]*Dottorato Regionale in Scienze della Terra Pegaso, Via Santa Maria, 53, Pisa 56126, Italy;* [f]*Dipartimento di Scienze dell'Ambiente e del Territorio e di Scienze della Terra, Università di Milano-Bicocca, Piazza della scienza, 4, Milan 20126, Italy;* [g]*Departamento de Paleontologia de Vertebrados, Museo de Historia Natural-UNMSM, 1256, Avenida Arenales, Lima 14, Peru;* [h]*Institut royal des sciences naturelles de Belgique, D.O. Terre et Histoire de la Vie, 29, rue Vautier, Brussels 1000, Belgium*

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Hundreds of fossil marine vertebrates cropping out at Cerro Colorado (Pisco Basin, Peru) are identified and reported on a 1:6500 scale geological map and in a joined stratigraphic section. All the fossils are from the lower strata of the Pisco Formation, dated in this area to the late middle or early late Miocene. They are particularly concentrated (88%) in the stratigraphic interval from 40 to 75 m above the unconformity with the underlying Chilcatay Formation. The impressive fossil assemblage includes more than 300 specimens preserved as bone elements belonging mostly to cetaceans (81%), represented by mysticetes (cetotheriids and balaenopteroids) and odontocetes (kentriodontid-like delphinidans, pontoporiids, ziphiids, and physeteroids, including the giant raptorial sperm whale *Livyatan melvillei*). Seals, crocodiles, sea turtles, seabirds, bony fish, and sharks are also reported. Isolated large teeth of *Carcharocles* and *Cosmopolitodus* are common throughout the investigated stratigraphical interval, whereas other shark teeth, mostly of carcharinids, are concentrated in one sandy interval. This work represents a first detailed census of the extraordinary paleontological heritage of the Pisco Basin and the basis for future taphonomic, paleoecological, and systematic studies, as well as a much needed conservation effort for this extremely rich paleontological site.

**Keywords:** paleontological heritage; marine vertebrates; fossils; Miocene; Peru

*Corresponding author. Email: bianucci@dst.unipi.it



## 1. Introduction

The Pisco Formation (middle Miocene–late Pliocene, southern Peru) is known for its exceptional fossil record of marine vertebrates. This is perhaps the most significant record in the world for the Neogene, due to the extraordinary preservation, the elevated concentration of fossils, and their high diversity, including sharks and bony fish, marine turtles and crocodiles, seabirds, baleen and toothed whales, seals, and marine sloths.

Since the 1980s several studies have demonstrated that these fossils are concentrated in some restricted areas, which represent the main vertebrate-bearing fossil localities of the Pisco Formation. Most of the past studies focused on the description of the most significant fossils collected (e.g. Acosta-Hospitaleche, Altamirano-Sierra, & Stucchi, 2011; Acosta-Hospitaleche & Stucchi, 2005; Altamirano-Sierra, 2013; Amson, Argot, McDonald, & Muizon, 2014; Amson & Muizon, 2014; Amson, Muizon, Laurin, Argot, & Buffrénil, 2014; Amson, Muizon, Domning, Argot, & Buffrénil, 2015; Bianucci, Lambert, & Post, 2010; Bisconti, 2012; Bouetel & Muizon, 2006; Chávez, Stucchi, & Urbina, 2007; Cheneval, 1993; Ehret et al., 2012; Göhlich, 2007; Lambert, Bianucci, & Beatty, 2014; Lambert, Bianucci, & Muizon, 2008; Lambert, Bianucci, & Post, 2009; Lambert, Bianucci, & Post, 2010; Lambert, Bianucci, Post, Muizon, et al., 2010; Lambert & Muizon, 2014; Lambert, Muizon, & Bianucci, 2013, 2015; McDonald & Muizon, 2002; Muizon, 1981, 1984, 1988, 1993; Muizon & Domning, 2002; Muizon, Domning, & Ketten, 2002; Muizon & McDonald, 1995; Muizon, McDonald, Salas, & Urbina, 2003; Muizon, McDonald, Salas, & Urbina, 2004a, 2004b; Parham & Pyenson, 2010; Pilleri, 1989–1990; Stucchi, 2002, 2003, 2008a, 2008b; Stucchi & Emslie, 2005; Stucchi & Urbina, 2004, 2005a, 2005b; Stucchi, Urbina, & Giraldo, 2003; Urbina & Stucchi, 2005a, 2005b), but data about the diversity of the entire fossil assemblages were published only for some taxonomic groups (e.g. odontocetes in Muizon, 1984, 1988 and pinnipeds in Muizon, 1981) or as preliminary faunal lists (e.g. Bianucci et al., 2010). Moreover, these studies generally lack a detailed geological and stratigraphical background, thus leaving unresolved the vertical and horizontal distribution of the fossils in the exposed strata. The first attempt to census the fossil vertebrates in the Pisco Formation was made by Muizon and DeVries (1985). Two decades later, Brand, Esperante and colleagues (Brand, Esperante, Chadwick, Poma, and Alomía, 2004; Esperante, Brand, Nick, Poma, and Urbina, 2008; Esperante, Brand, Chadwick, & Poma, 2015), evidenced an extraordinary concentration of specimens in several localities of the Pisco Formation, but these papers were limited to baleen whales and, consequently, did not provide any useful information about the faunal diversity of these highly fossiliferous areas. With a different approach, Brand, Urbina, Chadwick, DeVries, and Esperante (2011) attempted to place some published fossil vertebrates of the Pisco Formation along several measured stratigraphic sections; their work provided a rough indication of the fossil distribution, only reporting a non-exhaustive list of fossils, some of which were not correctly placed along the stratigraphic sections (Lambert & Muizon, 2014).

The aim of this work is to present for the first time a detailed map reporting all fossil vertebrates cropping out at Cerro Colorado, the locality where the holotypes of the giant raptorial feeding sperm whale *Livyatan melvillei* (Lambert, Bianucci, Post, Muizon, et al., 2010), the long-snouted beaked whale *Messapicetus gregarius* Bianucci et al., 2010, and the sea turtle *Pacifichelys urbinai* Parham & Pyenson, 2010 were found.

## 2. Geological and stratigraphic setting

### 2.1. *Regional geology*

The Peruvian margin is generally recognized as a long-lived convergent margin, with the oceanic Nazca Plate subducting approximately eastward below the continental South American Plate.

This oblique tectonic collision developed a composite transform-convergent margin characterized by normal and strike-slip faults that formed a number of elongated extensional/pull apart basins along the western margin of Peru (Dunbar, Marty, & Baker, 1990; León, Aleman, Torres, Rosell, & De La Cruz, 2008; Thornburg & Kulm, 1981; Zúñiga-Rivero, Klein, Hay-Roe, & Álvarez-Calderon, 2010). On the central coast of Peru, the (East) Pisco basin formed in the forearc between 13°30′ and 15°S; it is separated from the immediately adjacent West Pisco basin, located on the slope, by a basement high (Thornburg & Kulm, 1981). Its filling succession shows extensive normal and transtensional faulting, which is the result of the strong coupling and prominent oblique convergence between the subducting oceanic slab and the overriding plate (León et al., 2008 and references therein). The tectonic structure of the Peruvian margin has not only been affected by the subduction of normal oceanic crust, but also disrupted by collision and subduction of the aseismic Nazca Ridge (Hampel, 2002), which produced rapid uplift and inversion of the basin starting from latest Pliocene/earliest Pleistocene time (Hsu, 1992; Macharé & Ortlieb, 1992; Pilger, 1981).

### 2.2. *Stratigraphy*

The infill of the Pisco basin is composed of four main stratigraphic units separated by three major breaks of the basin sedimentary record; from the oldest to the youngest, these units are the Paracas Group, the Otuma Formation, the Chilcatay Formation, and the Pisco Formation (DeVries, 1998). The geological map of the Cerro Colorado study area (Di Celma et al., in press) shows two important angular unconformities in the exposed succession, probably related to a combination of eustatic sea-level changes and regional tectonic movements. The first one is the interformational unconformity between the Oligo-Miocene Chilcatay Formation and the overlying Pisco Formation. The second one is a low-angle intraformational erosional discontinuity that allows the subdivision of the Pisco stratigraphic section, as exposed at Cerro Colorado, into two informal allomembers. The lower allomember is 75 m thick and consists of nearshore conglomerates and thoroughly bioturbated fine-grained sandstones, gradually succeeded by diatomites, diatomaceous mudstones, and minor additions of sandstones, dolomitic horizons, and ash layers. The upper allomember, exceeding 125 m in thickness, is exposed in the upper half of the Cerro Colorado hill and along the eastern portion of the study area; it may be subdivided into two main lithological packages. The lower package, up to 50 m thick, consists of gray and orange, very fine- to medium-grained sandstones displaying abundant evidence of current and wave reworking. The upper package is at least 75 m thick and mostly composed of finely laminated gray-white diatomite with minor interbedded sandstones, dolomitic horizons, and ash layers.

Eight major stratigraphic marker beds, representing a powerful tool to correlate isolated outcrops within the stratigraphic context of the Pisco Formation, have been defined throughout the Cerro Colorado study area. In ascending stratigraphic sequence, they are the Nazca, Tiwanacu, Quechua, Wari, Paracas, Inca, Ica-Chincha, and T17 marker beds. A detailed description of these *beds* is provided by Di Celma et al. (in press).

### 2.3. *Chronostratigraphic framework*

Based on the discovery of a rich mollusk level containing the bivalve *Anadara sechurana* (Olsson, 1932), Bianucci et al. (2010) and Lambert, Bianucci, Post, Muizon, et al. (2010) referred to the late middle Miocene (ca 12–13 Ma) the strata containing the holotype of *L. melvillei* and the specimens of *M. gregarius* described from Cerro Colorado. The *A. sechurana* level is here placed by us in the lower allomember, about 47 m above the basal angular unconformity. This

age fully agrees with Dunbar et al. (1990) and is just a bit younger than DeVries (1998, 2001) in respect to the ones reported for the basal deposits of the Pisco Formation.

The presence of the pontoporiid *Brachydelphis mazeasi* (Muizon, 1988) and of the ziphiid *M. gregarius* in the lower allomember of Cerro Colorado further supports the late middle Miocene age for this part of the section, as these species are also described from Cerro la Bruja, a locality where one of the oldest levels (ca 14–12 Ma) of the Pisco Formation is preserved (Bianucci et al., 2010; DeVries, 1998; Muizon, 1988).

Otherwise, preliminary biostratigraphical analyses based on diatoms support an early late Miocene age (early Tortonian) for the lower allomember (Di Celma et al., in press). Interestingly, the sister-taxon of *M. gregarius* is *Messapicetus longirostris* (Bianucci, Landini, & Varola, 1992) which is from the early Tortonian of Italy (Bianucci, Landini, & Varola, 1994). Nevertheless more detailed biostratigraphic studies and eventually also radiometric dating are needed to better constrain the age of this fossil assemblage.

## 3. Study area and methods

An area of approximately 12 $km^2$ at Cerro Colorado in Ica Region, southern Peru, has been investigated in detail since 2006 during 7 successive field campaigns. Fossils from this area were all found by systematic surface prospecting of the exposures and their exact location was carefully recorded using hand-held global positioning system (*GPS*) *receivers*. Detailed taphonomic observations and a preliminary identification of each surveyed fossil specimen were made in the field. On the whole, this area was roughly uniformly investigated, but special attention was given to a restricted area (ca 500 m by 500 m) around the *L. melvillei* locality, in order to record all exposed isolated shark teeth and bone fragments.

Systematic identifications in the field were made more complicated due to the incompleteness of specimens related to recent erosion (more intense in some areas, such as along steep slopes) and partial burial affecting most specimens.

Several specimens were partially excavated for a more accurate description and identification. At the end of the field observation, these were covered with sediment to avoid further erosion. A few highly significant specimens were collected and deposited in the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM) in Lima for preparation and study.

In the field, special attention was paid to avoid mapping different disarticulated bones of the same animal as belonging to different individuals: size, morphology, fossilization, preservation aspect, and relative position in the stratigraphic column were compared. Bones that were close but originated from different stratigraphic horizons were obviously referred to distinct animals. Isolated bones that were not found *in situ* and therefore lacked any precise stratigraphical context were not taken into account.

In addition to the completeness of the specimen, the accuracy of the filed systematic determination depends upon the preservation and exposure of diagnostic elements (e.g. for cetaceans, ear bones are often sufficient to identify the family, whereas vertebrae and ribs are much less significant). Determination to species level was possible for several specimens (e.g. the ones referred to *M. gregarius*), thanks to the collection, laboratory preparation, and detailed study of part of the material.

All fossil specimens were reported on a 1:6500 scale geological map and positioned along the sequence of distinctive marker beds (Di Celma et al., in press) and in a measured stratigraphic section, thus providing a framework for the spatial and temporal placement of all data, observations, samples, and specimens collected during the study. The stratigraphic accuracy for the positioning of specimens along the measured section ranges from $\pm$ 0.4 to $\pm$ 3 m. The horizontal and vertical distribution of all recorded fossils is reported in the Main Map.

Concerning the isolated shark teeth, only those belonging to *Carcharocles* and *Cosmopolitodus* were reported on the map and along the stratigraphic column. However, unlike the bone remains, they do not necessarily indicate the death of the animal (one shark loses several thousand teeth during its lifetime). Moreover the original concentration of outcropping large shark teeth was observed to decrease over the course of our subsequent field campaigns, due to their continuous illegal collection. In the stratigraphic section, a significant sandy bed displaying an elevated concentration of shark teeth and bones is also reported.

Vertebrate specimens with precise GPS coordinates associated, that were deposited at the MUSM prior to the beginning of this study, were also included in the map. Other previously collected specimens with rough stratigraphic data associated were only taken into account for reconstructing the total vertebrate assemblage of Cerro Colorado.

Being beyond the aim of this work, detailed taphonomic and paleoecological observations are not reported here and will be discussed in a future paper.

## 4. Overall composition of the vertebrate assemblage

In total 318 specimens preserved as bone elements were recorded in the vertebrate assemblage of Cerro Colorado. The assemblage is dominated by cetacean remains (81% of the specimens), belonging to mysticetes (39%), odontocetes (23%) and indeterminate cetaceans (19%) (Figure 1).

Among mysticetes, a medium size (5–8 m) undescribed cetotheriid larger than *Piscobalaena nana* (Pilleri & Siber, 1989) is the most common taxon of Cerro Colorado. Furthermore, several complete to incomplete articulated skeletons of this taxon were found. In total, cetotheriid remains represent 18% of the entire vertebrate assemblage, as the indeterminate mysticetes (18%), whereas larger size balaenopteroids are relatively rarer (3%). The odontocete assemblage is more diversified, consisting of stem physeteroids (2%), ziphiids (5%), pontoporiids (9%), kentriodontid-like delphinidans (2%), indeterminate delphinidans (2%), and indeterminate odontocetes (3%). Physeteroids include (1) the holotype of *L. melvillei* (an almost complete skull, incomplete mandibles, nine detached teeth, and other tooth fragments) (Lambert, Bianucci, Post, Muizon, et al., 2010), (2) two specimens related to *Acrophyseter* (including skulls), and (3) a partial skeleton belonging to an undescribed genus (recently collected for preparation and study). Ziphiids are mainly represented by isolated skulls, in some cases with articulated mandibles, of *M. gregarius*. The holotype and most of the described referred material (represented by males, females, and one calf) of this species originate from Cerro Colorado (Bianucci et al., 2010). After the publication of this material, additional remains of *M. gregarius* were discovered at Cerro Colorado, including several skulls with associated postcranial remains. The ziphiid record in Cerro Colorado also includes a fragmentary skull, recently collected for preparation and study, showing some affinities with the South African species *Nenga nasalis* (Bianucci, Lambert, & Post, 2007). Kentriodontid-like delphinidans include two well-preserved skulls, belonging to two distinct new genera and species, as well as other more fragmentary remains. Pontoporiids are represented by three specimens referable to an undescribed *Pliopontos*-like species and several specimens referred to *Brachydelphis*. Among the latter, some well-preserved short-snouted skulls, sometimes with associate postcranial skeleton, were referred to *B. mazeasi*, whereas a fragmentary fetus and several isolated periotics could not be identified at the species level.

Non-cetacean marine vertebrates are represented by pinnipeds (4%), sea turtles (4%), longirostrine marine crocodylians (1%), seabirds (4%), sharks and rays (2%, excluding isolated teeth), and bony fish (4%).

The pinniped record consists of a skull with associated vertebral column and ribs, as well as several other fragmentary specimens, including an articulated skeleton, a fragmentary skull with

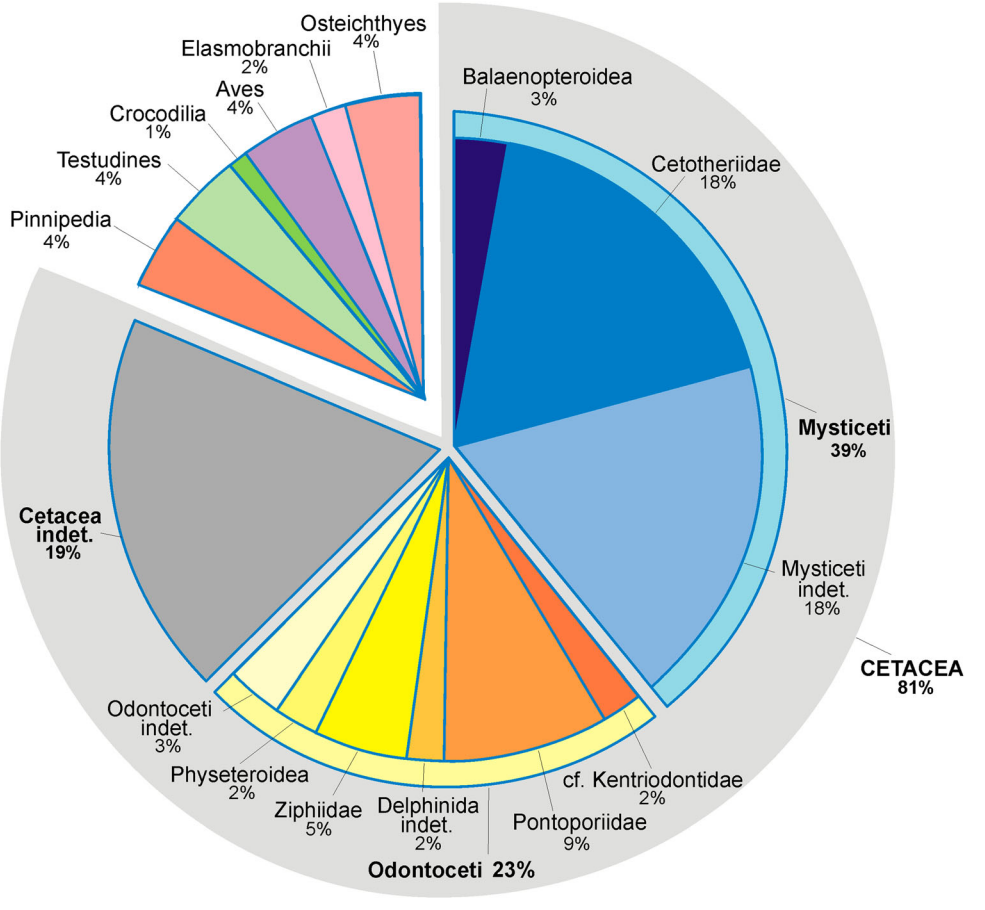


Figure 1. Quantitative composition of the fossil vertebrate assemblage from the Pisco Formation in Cerro Colorado, based on systematic surface prospecting and on a few fossils whose GPS coordinates are unknown. Isolated teeth of Elasmobranchii and fragmentary remains of indeterminate vertebrates are not considered.

associated mandible, and two isolated mandibles, all belonging to an indeterminate seal (family Phocidae).

Sea turtles are represented by several well-preserved partial skeletons (including skulls) of *P. urbinai*. Here again the holotype and most of the significant specimens described by Parham and Pyenson (2010) were found in Cerro Colorado.

Crocodiles are reported on the basis of a partial skeleton embedded in a nodule and some fragmentary postcranial bones.

Seabird remains include some exquisitely well-preserved skulls and/or postcranial skeletons belonging to two undescribed new species of booby (*Sula*, Sulidae) and other fragmentary bones of indeterminate cormorants (family Phalacrocoracidae) and procellarids.

Significant shark remains include teeth with associated vertebrae of *Comopolitodus hastalis* and indeterminate carcharinids. More than 3500 isolated elasmobranch teeth, mostly collected from a sandy level with a high concentration in shark teeth and bony fish remains, belong to: (1) carchariniformes (79.5%), represented by carcharinids (78%), and sphyrnids (1.5%); (2) lamniformes (14.5%), represented by lamnids (12.5%), odontaspidids (1.5%), and otodontids (0.5%); (3) myliobatids (6%); and (4) very rare (one tooth for each family) pristids and squatinids

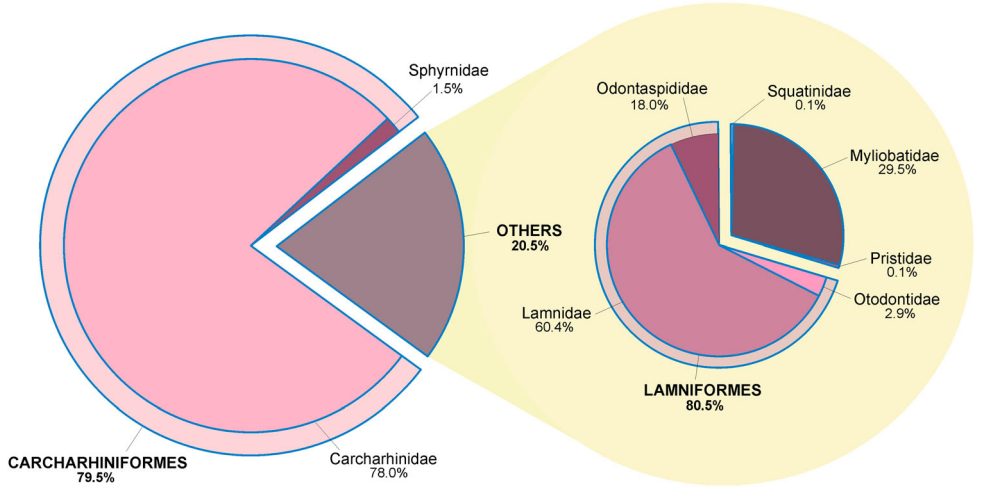


Figure 2. Quantitative composition of the fossil shark assemblage from the Pisco Formation in Cerro Colorado, based on 3586 isolated teeth.

(Figure 2). Significant remains of bony fish belong to scombrids (aff. *Thunnus* sp.) and to an indeterminate sciaenid.

## 5. Fossil distribution

### 5.1. *Spatial distribution on the ground*

On the whole, fossil vertebrates appear not to be uniformly distributed across the mapped area: in some areas, such as at the NE and SW of the Cerro Colorado hill, their concentration is low, whereas fossils are apparently absent at the top of the hill (Figure 3). Such a non-homogenous distribution may be due to: (1) the recent morphological changes of the landscape (on a drop off the fossils exhibit a lower exposition and are subjected to a greater erosion); (2) the covering of fossil-bearing outcrops with recent aeolian or landslide deposits; (3) and the non-homogenous vertical and/or horizontal distribution of fossils in the strata. Low fossil concentration at the SW of the Cerro Colorado hill is probably due to 1 and 2, whereas the absence of fossils at the top and the low concentration at the NE of the hill are probably due to 3. The apparently higher concentration of fossils around the *L. melvillei* locality is at least partly due to the more intense prospecting of this restricted area (see Methods section).

When analyzed separately, odontocetes and mysticetes on the whole display the same distribution pattern as all other vertebrates. However, among mysticetes, balaenopteroid remains are absent in the plain north of the hill, whereas no cetotheriid is recorded on the hill, above the intraformational angular unconformity separating the lower from the upper allomember. Among odontocetes, all physeteroids apart from the *Livyatan* holotype were discovered to the south of the hill. Considering other vertebrates, pinnipeds are only present on the hill, above the angular unconformity, where bony remains of reptiles, seabirds, bony fish, and sharks were not found. *Carcharocles* and *Cosmopolitodus* teeth show a wide distribution.

### 5.2. Stratigraphaic distribution

The stratigraphic distribution of the fossil vertebrates in Cerro Colorado appears highly non-randomly organized, with the highest concentration (88%) of recorded remains in the lower

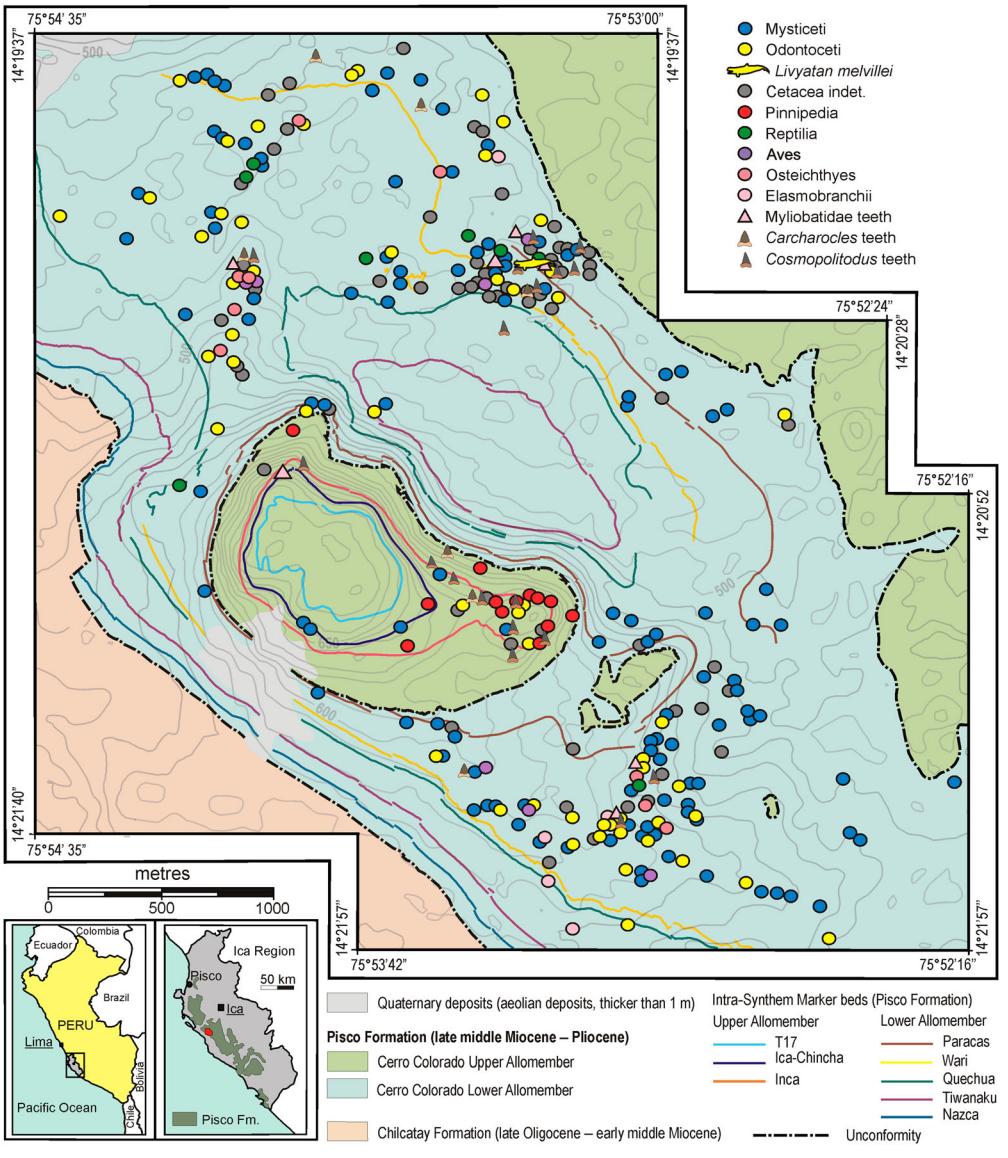


Figure 3. Map of the investigated area of Cerro Colorado showing the whole fossil vertebrate distribution.

allomember, between 40 and 75 m above the basal unconformity with the Chilcatay Formation (Figure 4). Isolated shark teeth of *Carcharocles* and *Cosmopolitodus* are also common in these fossiliferous strata. In this stratigraphic interval, two distinct peaks were identified: the most pronounced between 60 and 65 m (27% of all the fossils found, including the *L. melvillei* holotype) and the other between 45 and 50 m (15%). A similar distribution is observed when analyzing separately each vertebrate group (excluding the pinnipeds, absent in the lower allomember) with some small differences perhaps due to the low, less statistically representative number of specimens. The above-mentioned 1 m-thick sandy bed is extremely rich in elasmobranch teeth and fish bones are located in this lower allomember, about 59 m above the basal angular unconformity.

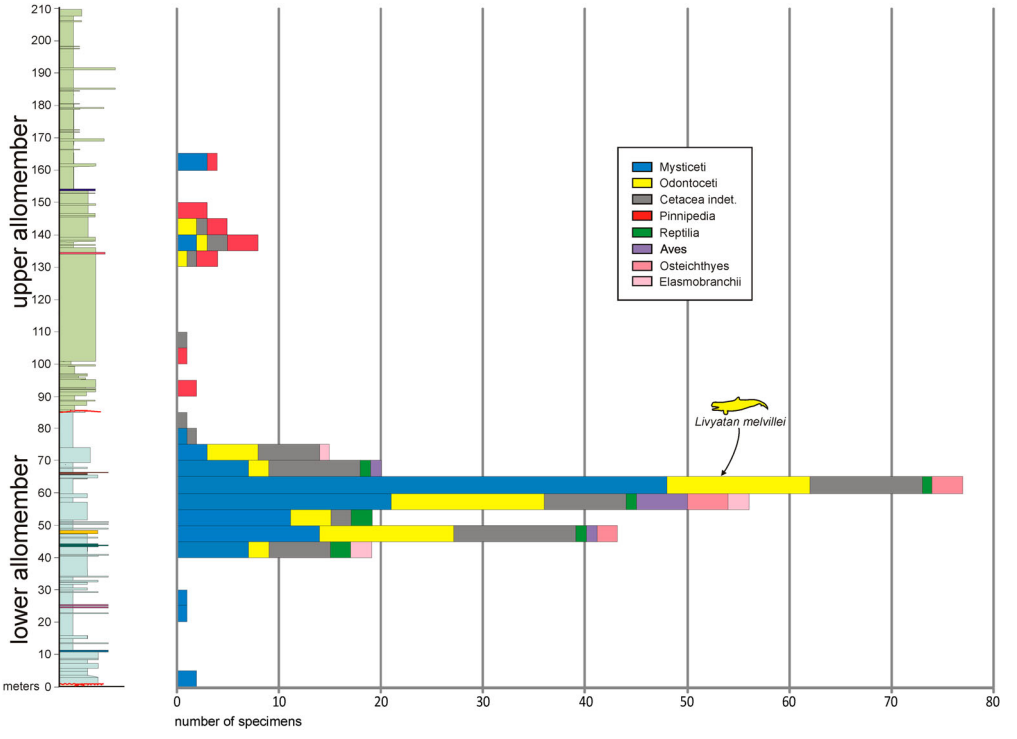


Figure 4. Stratigraphic distribution of fossil vertebrates in Cerro Colorado.

Another smaller peak (7% of all fossils) is observable in the upper allomember stratigraphic interval, between 130 and 150 m above the basal angular unconformity. As for all the upper allomember, the fossil bone assemblage of this stratigraphic interval consists of pinnipeds and cetaceans. All identified mysticete remains of the upper allomember strata are referred to balaenopteroids; very common in the lower allomember, cetotheriids are apparently absent. Whereas bony remains of reptiles, seabirds, bony fish, and sharks are absent from the upper allomember, isolated shark teeth (but only of *Carcharocles* and *Cosmopolitodus*) are found near pinniped and cetacean remains.

Outside these high concentration levels, fossil vertebrates are relatively rare and represent only 5% of the total fossil vertebrate assemblage of the section. More specifically, fossil vertebrates are totally absent in the lower allomember between 5 and 20 m above the basal unconformity and in the whole upper portion of the upper allomember (starting from about 165 m above the basal unconformity).

To interpret the non-uniform distribution of fossil vertebrates in the stratigraphic section, it is necessary to consider the role of the non-homogenous exposure of the strata in the study area. Where the strata occasionally cross the surface with a high angle in correspondence with the drop off, as noted above, the number of fossils discovered could be lower due to their more limited exposure and greater rate of erosion. Such considerations are certainly applicable for the beds in the lower allomember between 40 and 75 m above the basal unconformity. The high fossil concentration in the areas N and SE of the Cerro Colorado hill corresponds to strata crossing the topography with a low angle, whereas an apparently lower fossil concentration appears on the almost vertical NE and SW slopes of the hill. Instead, fossil vertebrates are almost absent in the lower and upper portions of the stratigraphic section, respectively, to the NE and at

the top of the hill, despite the fact that beds crop out almost parallel to the ground in these areas. At least for these cases we can assume that the low number of fossils reported in the section corresponds to a real low concentration in the corresponding strata. Therefore, it is reasonable to propose that the non-uniform distribution of fossil vertebrates in the stratigraphic section is mainly due to vertical changes in fossils concentration.

## 6. Conclusion

Focusing on the lower portion (late middle or early late Miocene) of the Pisco Formation cropping out at Cerro Colorado (the locality of the giant raptorial sperm whale *L. melvillei*), this work provides for the first time a combined quantitative and qualitative evaluation of the fossil vertebrates from a Pisco Formation locality (Figure 5).

Thanks to a detailed geological and stratigraphic study undertaken concomitantly (an important aspect) to the prospection and mapping of fossil vertebrates, all the fossils are reported on a geological map and along the related stratigraphic section. Taken together, these two data-sets provide a detailed and unique overview of the spatial and stratigraphic vertebrate distribution. In particular, an outstandingly elevated concentration (88% of all fossils) is observed from 40 to 75 m above the angular unconformity on the underlying Chilcatay Formation.

The systematic determination of more than 300 specimens preserved as bony elements yielded important information on the composition of the fossil assemblage. Most of these fossils belong to cetaceans (81%), represented by (1) mysticetes (39%), including cetotheriids (18%). and balaenopteroids (3%) and (2) odontocetes (23%), including kentriodontid-like delphinidans (2%), pontoporiids (9%), indeterminate delphinidans (2%), ziphiids (5%), and physeteroids (2%). Pinnipeds (4%), sea turtles (4%), crocodiles (1%), seabirds (4%), bony fish (4%), and sharks (2%) are also reported. Isolated large teeth of *Carcharocles* and *Cosmopolitodus* are common in all the investigated areas of the locality, whereas other shark teeth, most of them referred to carcharinids, are concentrated in one sandy bed.

Data reported in this work represent a unique basis for the development of different research topics: (1) the reconstruction of the ecological structure of the vertebrate assemblage at Cerro Colorado, with a special emphasis on the trophic relationships and the impact of top predators (e.g. *Livyatan* and *Carcharocles*) on this ancient marine ecosystem; (2) the taphonomic analysis of the exceptional conservation of this fossil assemblage; and (3) the more punctual systematic studies of significant specimens belonging to new taxa (several cetacean specimens have already been collected and are currently under preparation), in a stratigraphic and geological framework which is more robust than previous work on the vertebrates of the Pisco Formation.

This work represents the first step of a long-term multidisciplinary project foreseeing the realization of similar maps of fossil vertebrates from other localities of the Pisco Formation (e.g. Cerro Los Quesos, see Lambert et al., 2009) and also from the older and seemingly fossiliferous Chilcatay Formation (e.g. Ullujaya, see Bianucci, Urbina, & Lambert, 2014; Lambert, Bianucci, & Urbina, 2014; Lambert et al., 2015).

Finally, in order to trigger actions to preserve and promote this extraordinary paleontological heritage, this paper represents the first attempt at compiling highly accurate data on the occurrence of marine vertebrates within the Pisco Formation. Indeed, this comprehensive study may also constitute the first step toward an improved management and conservation of Peruvian paleontological heritage, through: (1) the collection of a large amount of paleontological and geological data demonstrating the richness and uniqueness of the Pisco basin fossil localities as well as their scientific significance, as a means to producing plans for conservation and future research; (2) the implementation of a general database for the paleontological content of Pisco localities. Such a database will be housed at the MUSM and access will be provided to the community


Figure 5. Fossil vertebrates from the Pisco Formation in Cerro Colorado. (a) Partially articulated skeleton of the ziphiid *M. gregarius*. (b) Complete and articulated skeleton of a kentriodontid-like delphinoid. (c) Skull and mandible of the holotype of the physeteroid *L. melvillei*. (d), (e), and (f) Complete and articulated skeletons of cetotheriid mysticetes. (g) Skull and partial skeleton of the sea turtle *P. urbinai*. (h) Several associated shark teeth belonging to the same individual of *C. hastalis*.

for projects involving research, mining, construction, recreation, and tourism in the Pisco Basin area; and (3) collaborative projects with regional and national Peruvian authorities for the application of this conservation model to other paleontological localities in Peru.

Therefore, this work should better be considered as the first step for the future study and conservation of fossil marine vertebrates from the Peruvian southern coast, more than the final result of multiple field campaigns.

## Software

The geological map was compiled by scanning hand drafts as black and white TIF files, and then digitizing the linework using the Corel Draw X3 graphics package. By using the GIS Data processing application Global Mapper 12, contour lines for the topographic base map were generated from digital elevation models based on the Shuttle Radar Topography Mission 26 (SRTM), as released by the United States Geological Survey (SRTM3 USGS version 2.1). Positions of fossil specimens were superimposed on the outcrop pattern of distinctive marker bed horizons using Global Mapper 12 to convert a Google Earth kmz file containing their position to Corel Draw.

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No potential conflict of interest was reported by the authors.

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## References

Acosta-Hospitaleche, C., Altamirano-Sierra, A., & Stucchi, M. (2011). Variaciones morfológicas del tarsometatarso de los pingüinos (Aves, Sphenisciformes) de la secuencia estratigráfica de la Formación Pisco (Mioceno-Plioceno), Perú. *Revista mexicana de ciencias geológicas*, *28*, 290–300.

Acosta-Hospitaleche, C., & Stucchi, M. (2005). Nuevos restos de Spheniscidae (Aves, Sphenisciformes) procedentes de la costa del Perú. *Revista Española de Paleontología*, *20*, 1–5.

Altamirano-Sierra, A. J. (2013). Primer registro de pelícano (Aves:Pelicanidae) para el Mioceno tardio de la formacion Pisco, Perù. *Bulletin de l'Istitut Français d'Études Andines*, *42*, 1–12.

Amson, E., Argot, C., McDonald, H. G., & Muizon, C. de. (2014). Osteology and functional morphology of the forelimb of the marine sloth Thalassocnus (Mammalia, Tardigrada). *Journal of Mammalian Evolution*. doi:10.1007/s10914-014-9268-3

Amson, E., & Muizon, C. de. (2014). A new durophagous phocid (Mammalia: Carnivora) from the late Neogene of Peru and considerations on monachine seals phylogeny. *Journal of Systematic Palaeontology*, *12*, 523–548. doi:10.1080/14772019.2013.799610

Amson, E., Muizon, C. de, Domning, D. P., Argot, C., & Buffrénil, V. de. (2015). Bone histology as a clue for resolving the puzzle of a dugong rib in the Pisco Formation, Peru. *Journal of Vertebrate Paleontology*. doi:10.1080/02724634.2014.922981

Amson, E., Muizon, C. de, Laurin, M., Argot, C., & Buffrénil, V. de. (2014). Gradual adaptation of bone structure to aquatic lifestyle in extinct sloths from Peru. *Proceedings of the Royal Society B: Biological Sciences*, *281*. doi:10.1098/rspb.2014.0192

Bianucci, G., Lambert, O., & Post, K. (2007). A high diversity in fossil beaked whales (Odontoceti, Ziphiidae) recovered by trawling from the sea floor off South Africa. *Geodiversitas*, *29*, 5–62.

Bianucci, G., Lambert, O., & Post, K. (2010). High concentration of long-snouted beaked whales (genus *Messapicetus*) from the Miocene of Peru. *Palaeontology*, *53*, 1077–1098. doi:10.1111/j.1475-4983.2010.00995.x

Bianucci, G., Landini, W., & Varola, A. (1992). *Messapicetus longirostris*, a new genus and species of Ziphiidae (Cetacea) from the late Miocene of 'Pietra Leccese' (Apulia, Italy). *Bollettino della Società Paleontologica Italiana*, *31*, 261–264.

Bianucci, G., Landini, W., & Varola, A. (1994). Relationships of *Messapicetus longirostris* (Cetacea, Ziphiidae) from the Miocene of South Italy. *Bollettino della Società Paleontologica Italiana*, *33*, 231–241.

Bianucci, G., Urbina, M., & Lambert, O. (2014). A new record of *Notocetus vanbenedeni* (Squalodelphinidae, Odontoceti, Cetacea) from the early Miocene of Peru. *Comptes Rendus Palevol*, *14*, 5–13. doi:10.1016/j.crpv.2014.08.003

Bisconti, M. (2012). Comparative osteology and phylogenetic relationships of *Miocaperea pulchra*, the first fossil pygmy right whale genus and species (Cetacea, Mysticeti, Neobalaenidae). *Zoological Journal of the Linnean Society*, *166*, 876–911. doi:10.1111/j.1096-3642.2012.00862.x

Bouetel, V., & Muizon, C. de. (2006). The anatomy and relationships of *Piscobalaena nana* (Cetacea, Mysticeti), a Cetotheriidae s.s. from the early Pliocene of Peru. *Geodiversitas*, *28*, 319–395.

Brand, L. R., Esperante, R., Chadwick, A. V., Poma, O., & Alomía, M. (2004). Fossil whale preservation implies high diatom accumulation rate in the Miocene-Pliocene Pisco Formation of Peru. *Geology*, *32*, 165–168. doi:10.1130/G20079.1

Brand, L. R., Urbina, M., Chadwick, A., DeVries, J. T., & Esperante, R. (2011). A high resolution stratigraphic framework for the remarkable fossil cetacean assemblage of the Miocene/Pliocene Pisco Formation, Peru. *Journal of South American Earth Sciences*, *31*, 414–425. doi:10.1016/j.jsames.2011.02.015

Chávez, M., Stucchi, M., & Urbina, M. (2007). El registro de Pelagornithidae (Aves: Pelecaniformes) y la avifauna neógena del Pacífico sudeste. *Bulletin de l'Institut Français d'Études Andines*, *36*(2), 175–197. doi:10.4000/bifea.3073

Cheneval, J. (1993). L'avifaune Mio–Pliocène de la Formation Pisco (Pérou). *Etude préliminaire. Documents des Laboratoires de Géologie, Lyon*, *125*, 85–95.

DeVries, T. J. (1998). Oligocene deposition and Cenozoic sequence boundaries in the Pisco Basin (Peru). *Journal of South American Earth Sciences*, *11*, 217–231. doi:10.1016/S0895-9811(98)00014-5

DeVries, T. J. (2001). Molluscan evidence for an Oligocene-Miocene age of 'Paracas' beds in southern Peru. *Boletín de la Sociedad Geológica del Perú*, *92*, 57–65.

Di Celma, C., Malinverno, E., Gariboldi, K., Gioncada, A., Rustichelli, A., Pierantoni, P. P., … Bianucci, G. (in press). Stratigraphic framework of the late Miocene to Pliocene Pisco formation at Cerro Colorado (Ica Desert, Peru). *Journal of Maps*. doi:10.1080/17445647.2015.1047906

Dunbar, R. B., Marty, R. C., & Baker, P. A. (1990). Cenozoic marine sedimentation in the Sechura and Pisco basins, Peru. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *77*, 235–261. doi:10.1016/0031-0182(90)90179-B

Ehret, D. J., Mac Fadden, B. J., Jones, D. S., DeVries, T. J., Foster, D. A., & Salas-Gismondi, R. (2012). Origin of the white shark *Carcharodon* (Lamniformes: Lamnidae) based on the upper Neogene Pisco Formation of Peru. *Paleontology*, *55*, 1139–1153. doi:10.1111/j.1475-4983.2012.01201.x

Esperante, R., Brand, L. R., Chadwick, A. V., & Poma, O. (2015). Taphonomy and paleoenvironmental conditions of deposition of fossil whales in the diatomaceous sediments of the Miocene/Pliocene Pisco Formation, southern Peru – a new fossil-lagerstätte. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *417*, 337–370. doi:10.1016/j.palaeo.2014.09.029

Esperante, R., Brand, L. R., Nick, K. E., Poma, O., & Urbina, M. (2008). Exceptional occurrence of fossil baleen in shallow marine sediments of the Neogene Pisco Formation, Southern Peru. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *257*, 344–360. doi:10.1016/j.palaeo.2007.11.001

Göhlich, U. B. (2007). The oldest fossil record of the extant penguin genus *Spheniscus* – a new species from the Miocene of Peru. *Acta Palaeontologica Polonica*, *52*, 285–298.

Hampel, A. (2002). The migration history of the Nazca ridge along the Peruvian active margin: A re-evaluation and some geological implications. *Earth and Planetary Science Letters*, *203*, 665–679. doi:10.1016/S0012-821X(02)00859-2

Hsu, J. T. (1992). Quaternary uplift of the Peruvian coast related to the subduction of the Nazca Ridge: 13.5 to 15.6 degrees south latitude. *Quaternary International*, *15/16*, 87–97. doi:10.1016/1040-6182(92)90038-4

Lambert, O., Bianucci, G., & Beatty, B. L. (2014). Bony outgrowths on the jaws of an extinct sperm whale support macroraptorial feeding in several stem physeteroids. *Naturwissenschaften*, *101*, 517–521. doi:10.1007/s00114-014-1182-2

Lambert, O., Bianucci, G., & Muizon, C. de. (2008). A new stem-sperm whale (Cetacea, Odontoceti, Physeteroidea) from the latest Miocene of Peru. *Comptes Rendus Palevol*, *7*, 361–369. doi:10.1016/j.crpv.2008.06.002

Lambert, O., Bianucci, G., & Post, K. (2009). A new beaked whale (Odontoceti, Ziphiidae) from the Middle Miocene of Peru. *Journal of Vertebrate Paleontology*, *29*, 910–922. doi:10.1671/039.029.0304

Lambert, O., Bianucci, G., & Post, K. (2010). Tusk bearing beaked whales from the Miocene of Peru: Sexual dimorphism in fossil ziphiids? *Journal of Mammalogy*, *91*, 16–26. doi:10.1644/08-MAMM-A-388R1.1

Lambert, O., Bianucci, G., Post, K., Muizon, C. de, Salas-Gismondi, R., Urbina, M., & Reumer, J. (2010). The giant bite of a new raptorial sperm whale from the Miocene epoch of Peru. *Nature*, *466*, 105–108. doi:10.1038/nature09067

Lambert, O., Muizon, C. de, & Bianucci, G. (2013). The most basal beaked whale *Ninoziphius platyrostris* Muizon, 1983: Clues on the evolutionary history of the family Ziphiidae (Cetacea: Odontoceti). *Zoological Journal of the Linnean Society*, *167*, 569–598. doi:10.1111/zoj.12018

Lambert, O., Bianucci, G., & Urbina, M. (2014). *Huaridelphis raimondii*, a new early Miocene Squalodelphinidae (Cetacea, odontoceti) from the Chilcatay Formation, Peru. *Journal of Vertebrate Paleontology*, *34*, 987–1004. doi:10.1080/02724634.2014.858050

Lambert, O., & Muizon, C. de. (2014). A new long-snouted species of the Miocene pontoporiid dolphin *Brachydelphis* and a review of the Mio-Pliocene marine mammal levels in the Sacaco Basin, Peru. *Journal of Vertebrate Paleontology*, *33*, 709–721. doi:10.1080/02724634.2013.743405

Lambert, O., Muizon, C. de., & Bianucci, G. (2015). A new archaic homodont toothed whale (Mammalia, Cetacea, Odontoceti) from the early Miocene of Peru. *Geodiversitas*, *37*, 79–108. doi:10.5252/g2015n1a4

León, W., Aleman, A., Torres, V., Rosell, W., & De La Cruz, O. (2008). Estratigrafía, Sedimentología y evolución tectónica de la cuenca Pisco Oriental. *Boletín INGEMMET, Serie D*, *27*, 144.

Macharé, J., & Ortlieb, L. (1992). Plio-quaternary vertical motions and the subduction of the Nazca Ridge, central coast of Peru. *Tectonophysics*, *205*, 97–108. doi:10.1016/0040-1951(92)90420-B

McDonald, H. G., & Muizon, C. de. (2002). The cranial anatomy of *Thalassocnus* (Xenarthra, Mammalia), a derived nothrothere from the Neogene of the Pisco formation (Peru). *Journal of Vertebrate Paleontology*, *22*, 349–365. doi:10.1671/0272-4634(2002)022[0349:TCAOTX]2.0.CO;2

Muizon, C. de. (1981). Les vertébrés fossiles de la Formation Pisco (Pérou). Première partie: Deux nouveaux Monachinae (Phocidae, Mammalia) du Pliocène de Sud-Sacaco. *Travaux de l'Institut Français d'Études Andines*, *22*, 1–160.

Muizon, C. de. (1984). Les Vertébrés de la Formation Pisco (Pérou). Deuxième partie: Les Odontocètes (Cetacea, Mammalia) du Pliocène inférieur de Sud-Sacaco. *Travaux de l'Institut Français d'Études Andines*, *27*, 1–188.

Muizon, C. de. (1988). Les Vertébrés fossiles de la Formation Pisco (Pérou). Troisième partie: Les Odontocètes (Cetacea, Mammalia) du Miocène. *Travaux de l'Institut Français d'Études Andines*, *42*, 1–244.

Muizon, C. de. (1993). Walrus-like feeding adaptation in a new cetacean from the Pliocene of Peru. *Nature*, *365*, 745–748. doi:10.1038/365745a0

Muizon, C. de, & DeVries, T. J. (1985). Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). *Geologische Rundschau*, *74*, 547–563. doi:10.1007/BF01821211

Muizon, C. de., & Domning, D. P. (2002). The anatomy of *Odobenocetops* (Delphinoidea, Mammalia), the walrus-like dolphin from the Pliocene of Peru and its palaeobiological implications. *Zoological Journal of the Linnean Society*, *134*, 423–452. doi:10.1046/j.1096-3642.2002.00015.x

Muizon, C. de., Domning, D. P., & Ketten, D. R. (2002). *Odobenocetops peruvianus*, the walrus-convergent delphinoid (Cetacea, Mammalia) from the lower Pliocene of Peru. *Smithsonian Contributions to Paleobiology*, *93*, 223–261.

Muizon, C. de, & McDonald, H. G. (1995). An aquatic sloth from the Pliocene of Peru. *Nature*, *375*, 224–227. doi:10.1038/375224a0

Muizon, C. de, McDonald, H. G., Salas, R., & Urbina, M. (2003). A new early species of the aquatic sloth *Thalassocnus* (Mammalia, Xenarthra) from the ate Miocene of Peru. *Journal of Vertebrate Paleontology*, *23*, 886–894. doi:10.1671/2361-13

Muizon, C. de, McDonald, H. G., Salas, R., & Urbina, M. (2004a). The youngest species of the aquatic sloth *Thalassocnus* and a reassessment of the relationships of the nothrothere sloths (Mammalia: Xenarthra). *Journal of Vertebrate Paleontology*, *24*, 287–397. doi:10.1671/2429a

Muizon, C. de, McDonald, H. G., Salas, R., & Urbina, M. (2004b). The evolution of feeding adaptations of the aquatic sloth *Thalassocnus*. *Journal of Vertebrate Paleontology*, *24*, 398–410. doi:10.1671/2429b

Olsson, A. A. (1932). Contributions to the Tertiary paleontology of northern Peru: Part 4, The Peruvian Oligocene. *Bulletins of American Paleontology*, *17*, 1–124.

Parham, J. F., & Pyenson, N. D. (2010). New sea turtle from the Miocene of Peru and the iterative evolution of feeding ecomorphologies since the Cretaceous. *Journal of Paleontology*, *84*, 231–247. doi:10.1666/09-077R.1

Pilger, R. H. (1981). Plate reconstructions, aseismic ridges, and low-angle subduction beneath the Andes. *Geological Society of America Bulletin*, *92*, 448–456. doi:10.1130/0016-7606(1981)92<448:PRARAL>2.0.CO;2

Pilleri, G. (1989–1990). *Beiträge zur Paläontologie der Cetaceen Perus + Beiträge zur Paläontologie der Cetaceen und Pinnpedier der Pisco Formation Perus, II, two parts, complete*. Berne: Hirnanatomisches Institut Ostermundigen.

Pilleri, G., & Siber, H. J. (1989). Neuer spattertiarer cetotherid (Cetacea, Mysticeti) aus der Pisco-Formation Perus. In G. Pilleri (Ed.), *Beitrage zur Palaontologie der Cetacean Perus* (pp. 108–115). Berne: Hirnanatomisches Institut, Ostermundigen.

Stucchi, M. (2002). Una nueva especie de *Spheniscus* (Aves: Spheniscidae) de la Formación Pisco, Perú. *Boletin de la Sociedad Geologica del Peru*, *94*, 17–24.

Stucchi, M. (2003). Los Piqueros (Aves: Sulidae) de la Formación Pisco, Perú. *Boletín de la Sociedad Geológica del Perú*, *95*, 75–91.

Stucchi, M. (2008a). Reporte preliminar de un cráneo de Pelagornithidae (Aves: Odontopterigyformes) de la base de la formación Pisco, Perú (Mioceno medio). *Bulletin de l'Institut Français d'Études Andines*, *37*(3), 580–582.

Stucchi, M. (2008b). Un cóndor del Mioceno tardío de la costa Peruana. *Boletin de Lima*, *152*, 141–146.

Stucchi, M., & Emslie, S. (2005). A new condor (Ciconiiformes, Vulturidae) from the late Miocene/early Pliocene Pisco formation, Peru. *The Condor*, *107*, 107–113. doi:10.1650/7475

Stucchi, M., & Urbina, M. (2004). *Ramphastosula* (Aves: Sulidae): A new avian genus from the early Pliocene of the Pisco formation, Peru. *Journal of Vertebrate Paleontology*, *24*, 974–978. doi:10.1671/0272-4634(2004)024[0974:RASANG]2.0.CO;2

Stucchi, M., & Urbina, M. (2005a). Nuevos restos de Procellariiformes fósiles de la Formación Pisco, Perú. *Boletín de la Sociedad Geológica del Perú*, *100*, 67–77.

Stucchi, M., & Urbina, M. (2005b). Evidence of a fossil stork (Ciconiidae) from the Late Miocene of the Pisco Formation, Peru. *Boletín de la Sociedad Geológica del Perú*, *100*, 63–66.

Stucchi, M., Urbina, M., & Giraldo, A. (2003). Una nueva especie de Spheniscidae del Mioceno tardío de la Formación Pisco, Perú. *Bulletin de l'Institut Français d'Études Andines*, *32*, 361–375.

Thornburg, T. M., & Kulm, L. D. (1981). Sedimentary basins of the Peru continental margin: Structure, stratigraphy, and Cenozoic tectonics from 6°S to 16° latitude. In L. D. Kulm, J. Dymond, E. J. Dasch, & D. M. Hussong (Eds.), *Nazca plate: Crustal formation and Andean convergence* (pp. 393–422). Boulder, CO: Geological Society of America, Memoir, 154.

Urbina, M., & Stucchi, M. (2005a). Evidence of a fossil stork (Aves: Ciconiidae) from the late Miocene of the Pisco Formation, Peru. *Boletin de la Sociedad Geológica del Perú*, *100*, 63–66.

Urbina, M., & Stucchi, M. (2005b). Los Cormoranes (Aves: Phalacrocoracidae) de la Formación Pisco, Perú. *Boletín de la Sociedad Geológica del Perú*, *99*, 41–49.

Zúñiga-Rivero, F. J., Klein, G. D., Hay-Roe, H., & Álvarez-Calderon, E. (2010). *The hydrocarbon potential of Peru*. Lima: BPZ Exploración & Producción S.R.L., 338p.